BOTANICAL MUSEUM LEAFLETS VOL. 30, NO. 2
SPRING 1984

ANATOMY OF NONCOSTAL PORTIONS OF LAMINA IN THE CYCLANTHACEAE (MONOCOTYLEDONEAE). *V*. TABLES OF DATA

GEORGE J. WILDER*

This is the last paper of a series which pertains to lamina anatomy in the Cyclanthaceae (Wilder, in press a, b, c, d). Each paper is based on the same fifty-three species and ten genera of the family. Collection localities have been listed (Tomlinson and Wilder, 1984). The present paper includes tables which document findings in all previous papers of the series. Tables are organized into four groups representing paper nos. *I–IV* of the series, respectively. Each group of tables is introduced by a synopsis of the paper which it represents.

INTRODUCTION TO TABLES 1–6
(Wilder, in press *a*)

The outer walls of ordinary epidermal cells exhibit inner noncutinized and outer cutinized regions, and are covered by a cuticle sensu stricto (Table 1). Noncostal portions of cyclanthaceous laminae are always hypostomatic, i.e., having the majority of stomata situated in the abaxial epidermis (Tables 2, 3). In noncostal parts of this epidermis, stomata are oriented within stomatal bands, and such bands are separated by interstomatal bands of four main kinds: (*1*) in interridge areas, bands located over superficially situated fiber strands of the mesophyll, (*2*) also in interridge areas, bands situated over the largest longitudinal veins, (*3*) bands occurring on abaxial ridges, and (*4*) bands of epidermal expansion tissue. Given a small strip of epidermis, it is sometimes possible to ascertain the following: whether it is adaxial or abaxial; if abaxial, whether portions thereof are from interridge areas, ridges, or expansion tissue, and

*Harvard Forest, Harvard University
Petersham, Massachusetts 01366
Present address: Cleveland State University, Dept. of Biology,
1983 East 24th Street, Cleveland, Ohio 44115

which portions from interridge areas occur over fiber strands and the largest veins; which are the abaxial and adaxial sides of the strip; which are its distal and basal ends, and its left and right sides relative to the lamina it came from. A cyclanthaceous stoma is normally encircled by four subsidiary cells, and the stoma and associated subsidiary cells are collectively called a stomatal complex (Tables 4–6). Subsidiary cells may differ from ordinary epidermal cells in numerous ways such as their shape and position, nature of inclusions, staining of outer cell walls, size of nuclei, and thickness and ornamentation of the cuticle. In four species the stomata exhibit polar perforations, i.e., large pores located within the distal and basal ends of the common wall between two associated guard cells. Cyclanthaceous stomata exhibit substantial dorsiventral symmetry.

TABLE 1.

GENERAL RANGE IN COMBINED THICKNESS OF CUTICLE AND CUTINIZED REGION (rounded off to nearest quarter micrometer)

Species	*Adaxial epidermis*	*Abaxial epidermis*
A. aff. *A. antioquiae* (coll. A)	0.75– 1.5	0.5 – 2
A. aff. *A. antioquiae* (coll. B)	1 – 1.5	0.5 – 1
A. cabrerae	2 – 3.25	0.75– 2.5
A. cayapensis	1.5 – 2.5	0.5 – 2
A. sp. nov. aff. *A. cupulifera* (coll. A)	1 – 1.5	0.5 – 1
A. sp. nov. aff. *A. cupulifera* (coll. B)	3 – 4.75	1 – 3.75
A. gamotepala	3.25– 7.25	1.5 – 6.25
A. hookeri	0.75– 1.5	<0.5 – 0.75
A. longitepala	1.5 – 2.5	0.75– 1.5
A. sp. nov. aff. *A. longitepala*	2.5 – 5.25	1.5 – 4.25
A. moritziana	2 – 3.75	0.75– 3
A. aff. *A. moritzi*[illegible]	3 – 4.25	1 – 2.5

TABLE 1 *(continued)*

GENERAL RANGE IN COMBINED THICKNESS OF CUTICLE AND CUTINIZED REGION (rounded off to nearest quarter micrometer)

Species	*Adaxial epidermis*	*Abaxial epidermis*
A. sp. nov. aff. *A. multistaminata*	1 – 2.5	0.5 – 1.5
A. peruviana	1.5 – 4.75	0.5 – 2.5
A. pycnantha	2.5 – 4.5	1 – 3
A. quinindensis	1 – 2.5	0.5 – 1
A. sp. nov. aff. *A. rhodea*	1.5 – 2.5	0.5 – 2
A. rigida	1.5 – 3	0.5 – 1.25
A. tetragona	1.5 – 3.75	0.75 – 1.5
A. urophylla	3 – 8.75	1.5 – 4.75
A. aff. *A. vaupesiana* (coll. A)	1.5 – 3.25	0.5 – 2
A. aff. *A. vaupesiana* (coll. B)	1.5 – 2.5	0.5 – 1.5
A. (Asplundia) sp. nov.	1 – 3	1 – 3.25
Ca. palmata	3.5 – 5.5	1 – 4
Cy. bipartitus	1 – 2	0.5 – 1.5
D. crinitum	1.5 – 3.5	1 – 2.5
D. dolichostemon	0.5 – 1.5	<0.5 – 0.5
D. globosum	1.5 – 2.5	1 – 3
D. grandifolium	0.5 – 1	0.5 – 2
D. harlingii	<0.5 – 0.5	<0.5 – 0.5
D. macrophyllum	1.5 – 5.75	0.75 – 3.25
D. mirabile	0.75 – 1.5	0.5 – 1.5
D. sp. nov. aff. *D. nanum*	1.5 – 3	1 – 2.5
D. rheithrophilum	1.5 – 3.75	1 – 3.75
D. schultesii	0.75 – 2.5	0.5 – 3.25
D. wallisii	0.5	0.25 – 0.5
D. sp. nov. (coll. A)		0.5 – 0.75
D. sp. nov. (coll. B)	0.5 – 1	0.5

TABLE 1 *(continued)*

GENERAL RANGE IN COMBINED THICKNESS OF CUTICLE AND CUTINIZED REGION (rounded off to nearest quarter micrometer)

Species	*Adaxial epidermis*	*Abaxial epidermis*
E. funifer	2.0 - 3.5	1 - 3.5
L. bierhorstii	1 - 3	0.5 - 1
L. integrifolia	3.75- 6.75	2.5 - 5.25
L. lancifolia	3 - 5	2.5 - 5
Sch. chorianthum	1 - 1.5	<0.5 - 0.5
Sph. acutitepala	3 - 4.75	1 - 7.25
Sph. crocea	3.25- 7.75	1.5 - 4.75
Sph. killipii	5 - 7.5	0.5 - 3
Sph. snidernii	6.25-13	1 - 3.75
Sph. woodsonii	5.25- 7.25	0.5 - 1
Sph. sp. nov. aff. *Sph. woodsonii*	3 - 5.25	1.5 - 3.25
Sph. sp. nov.	3.25- 6.25	0.5 - 3
St. anomala	7.75-12	3.75-12
St. stylaris	8.5 -12.5	4 -10.5
T. bissectus	1 - 6.5	1 - 5

TABLE 2

CONCENTRATION OF STOMATA AND LAMINA THICKNESS IN INTERRIDGE AREAS.*

	No. of stomata/mm² in the abaxial epidermis, adaxial epidermis, and both epidermides			Ratio of nos. of stomata/mm² - abaxial:adaxial	Lamina thickness - general range and midpoint of range (mm)	Lamina thickness - in nos. of cell layers
A. aff. *A. antioquiae* (coll. A)	213	4.0	217	53	0.18–0.29; 0.24	11–13
A. aff. *A. antioquiae* (coll. B)	267	2.8	270	95	0.23–0.34; 0.29	12–15
A. cabrerae	108	13	121	8.4	0.41–0.52; 0.46	17–20
A. cayapensis	155	3.1	158	50	0.31–0.45; 0.38	19–22
A. sp. nov. aff. *A. cupulifera* (coll. A)	131	0.31	132	421	0.16–0.20; 0.18	10–15
A. sp. nov. aff. *A. cupulifera* (coll. B)	169	0.31	169	542	0.20–0.29; 0.24	13–15
A. gamotepala	260	9.0	269	29	0.35–0.44; 0.40	16–19
A. hookeri	117	3.1	120	38	0.22–0.29; 0.26**	10–12**
A. longitepala	138	2.5	140	55	0.25–0.36; 0.30	11–14
A. sp. nov. aff. *A. longitepala*	176	5.6	181	31	0.31–0.39; 0.35	15–18
A. moritziana	118	4.7	122	25	0.23–0.29; 0.26	12–16

TABLE 2 *(continued)*

CONCENTRATION OF STOMATA AND LAMINA THICKNESS IN INTERRIDGE AREAS.*

	No. of stomata/mm² in the abaxial epidermis, adaxial epidermis, and both epidermides			Ratio of nos. of stomata/mm² - abaxial:adaxial	Lamina thickness - general range and midpoint of range (mm)	Lamina thickness - in nos. of cell layers
A. aff. *A. moritziana*	269	1.2	270	216	0.20–0.26; 0.23	11–14
A. sp. nov. aff. *A. multistaminata*	144	12	156	12	0.21–0.27; 0.24	11–13
A. peruviana	167	8.3	175	20	0.21–0.27; 0.24	11–12
A. pycnantha	166	4.0	170	41	0.30–0.37; 0.33	16–20
A. quinindensis					0.19–0.26; 0.23	11–13
A. sp. nov. aff. *A. rhodea*	156	0.93	157	167	0.20–0.23; 0.22	11–12
A. rigida	132	5.6	138	24	0.28–0.37; 0.32	14–15
A. tetragona	140	5.6	145	25	0.19–0.24; 0.22	12–15
A. urophylla	207	8.1	215	26	0.24–0.32; 0.28	15–18**
A. aff. *A. vaupesiana* (coll. A)	188	11	199	17	0.23–0.29; 0.26**	12–15**
A. aff. *A. vaupesiana* (coll. B)	107	8.4	116	13	0.30–0.34; 0.32	13–15
A. (Asplundia) sp. nov.	104	3.4	107	30	0.32–0.41; 0.36	12–14

Ca. palmata	269	1.2	270	215	0.18–0.26; 0.22	12–16
Cy. bipartitus	311	41	352	7.6	0.26–0.41; 0.33	14–16
D. crinitum	234	0.93	235	250	0.34–0.43; 0.39	20–27
D. dolichostemon	142	29	170	4.9	0.23–0.31; 0.27	14–16
D. globosum	261	0	261	ca. ∞	0.32–0.37; 0.35	12–14**
D. grandifolium	107	30	138	3.6	0.19–0.26; 0.22	9–12
D. harlingii	108	46	154	2.3		
D. macrophyllum	255	0.31	255	818	0.34–0.45; 0.40	19–21
D. mirabile	165	62	228	2.7	0.23–0.32; 0.28	11–14
D. sp. nov. aff. *D. nanum*	270	26	296	10	0.27–0.33; 0.30	12–14**
D. rheithrophilum	189	19	208	10	0.41–0.48; 0.44	14–18
D. schultesii	151	28	179	5.4	0.19–0.24; 0.22	10–14
D. wallisii	273	22	295	12	0.25–0.28; 0.27	12–15**
D. sp. nov. (coll. A)	71	8.1	79	8.7	0.28–0.33; 0.30	9–11
D. sp. nov. (coll. B)	194	9.0	203	21	0.28–0.36; 0.32	14–16
E. funifer	160	14	174	11	0.17–0.24; 0.20	10–13
L. bierhorstii	59	2.5	61	24	0.26–0.32; 0.29**	10–12**
L. integrifolia	91	26	117	3.5	0.37–0.46; 0.42	12–15
L. lancifolia	44	34	78	1.3	0.47–0.61; 0.54	12–17
Sch. chorianthum	144	0	144	ca. ∞	0.12–0.16; 0.14	8–9

TABLE 2 *(continued)*

CONCENTRATION OF STOMATA AND LAMINA THICKNESS IN INTERRIDGE AREAS.*

	No. of stomata/mm² in the abaxial epidermis, adaxial epidermis, and both epidermides			Ratio of nos. of stomata/mm² - abaxial:adaxial	Lamina thickness - general range and midpoint of range (mm)	Lamina thickness - in nos. of cell layers
Sph. acutitepala	236	0	236	ca. ∞	0.32–0.38; 0.35	15–17
Sph. crocea	164	0.62	164	262	0.29–0.48; 0.39	16–18
Sph. killipii	309	5.6	315	55	0.33–0.38; 0.36	16–18
Sph. snidernii	273	10	283	27	0.28–0.36; 0.32	15–17
Sph. woodsonii	188	0	188	ca. ∞	0.36–0.42; 0.39	16–17
Sph. sp. nov. aff. *Sph. woodsonii*	123	3.7	127	33	0.40–0.45; 0.43	22
Sph. sp. nov.	486	1.9	488	260	0.23–0.32; 0.27	12–14
St. anomala	105	0	105	ca. ∞	0.30–0.41; 0.36**	13–17**
St. stylaris	176	1.9	178	94	0.47–0.61; 0.54	18–22
T. bissectus	227	80	307	2.8	0.33–0.43; 0.38	17–20

*Stomatal frequencies were determined by studying mostly stained, but also unstained epidermal peels with the phase microscope at 100X. Stomata were counted on 3.21 mm² of a peel from each of the abaxial and adaxial epidermides, with the following exceptions (the two figures between each pair of parentheses indicate areas studied [mm²] of the abaxial and adaxial epidermides, respectively): *A. peruviana* (1.81, 1.81), *A. urophylla* (3.01, 3.21), *D. harlingii* (2.01, 3.21), and *D. mirabile* (2.01, 1.61). As often as possible on a peel, fields were studied which were laterally rather than longitudinally adjacent to one another, to maximize randomness of sampling, i.e., to avoid including the same stomatal or interstomatal band(s) in all samples. For certain species the concentration indicated for both epidermides is slightly different from the total of the separate indicated concentrations, because the total was computed and rounded off, prior to rounding off of the separate values. Lamina thickness in mm was determined only for cross sections. Thickness in numbers of cell layers was ascertained, using portions of longitudinal sections containing only epidermal cells and ordinary parenchyma cells.

**These values were obtained from study of unembedded material which was bleached in an aqueous solution of sodium hypochlorite, and mounted in glycerine. Remaining values were determined during study of stained, plastic-embedded material.

TABLE 3

STOMATAL RATIOS IN THE INTERRIDGE AREA*

	Percentage of species with low ratios (0–29)	Percentage of species with moderate ratios (30–99)	Percentage of species with high ratios (100 and higher)
Asplundia (22, 94)	45.5	36.4	18.2
Carludovica (1, 3)	–	–	100
Cyclanthus (1, 1)	100	–	–
Dicranopygium (13, 48)	76.9	–	23.1
Evodianthus (1, 1)	100	–	–
Ludovia (3, 3)	100	–	–
Schultesiophytum (1, 1)	–	–	100
Sphaeradenia (7, 42)	14.3	28.6	57.1
Stelestylis (2, 4)	–	50	50
Thoracocarpus (1, 1)	100	–	–

*In parentheses after the name of each genus are indicated the number of species considered, and the total number of species known, not including undescribed species collected by the writer.

TABLE 4

PERCENTAGES OF STOMATAL COMPLEXES IN THE ABAXIAL EPIDERMIS IN WHICH NEITHER, ONE, OR BOTH NONPOLAR SUBSIDIARY CELL(S) EXTEND(S) TO THE OUTER EDGE(S) OF THE ASSOCIATED CELL FILE(S).*

	Neither extends to outer edge	One extends to outer edge	Both extend to outer edge	One or both extend to outer edge(s) (column 2 + column 3)
A. aff. *A. antioquiae* (coll. A)	76.7	20.0	3.3	23.3
A. aff. *A. antioquiae* (coll. B)	85.3	13.3	1.3	14.7
A. cabrerae	24.0	47.3	28.7	76.0
A. cayapensis	94.7	5.3	0.0	5.3
A. sp. nov. aff. *A. cupulifera* (coll. A)	85.3	14.7	0.0	14.7
A. sp. nov. aff. *A. cupulifera* (coll. B)	95.3	4.7	0.0	4.7
A. gamotepala	67.3	28.0	4.7	32.7
A. hookeri	96.7	3.3	0.0	3.3
A. longitepala	78.7	20.7	0.7	21.3
A. sp. nov. aff. *A. longitepala*	75.3	22.7	2.0	24.7
A. moritziana	86.0	13.3	0.7	14.0

A. aff. *A. moritziana*	73.3	25.3	1.3	26.7
A. sp. nov. aff. *A. multistaminata*	76.7	21.3	2.0	23.3
A. peruviana	37.3	32.0	30.7	62.7
A. pycnantha (n=159)	70.4	24.5	5.0	29.5
A. quinindensis	80.0	18.0	2.0	20.0
A. sp. nov. aff. *A. rhodea*	97.3	2.7	0.0	2.7
A. rigida	60.0	33.3	6.7	40.0
A. tetragona	86.0	12.7	1.3	14.0
A. urophylla	66.7	29.3	4.0	33.3
A. aff. A. *vaupesiana* (coll. A)	68.7	26.7	4.7	31.3
A. aff. *A. vaupesiana* (coll. B)	79.3	20.0	0.7	20.7
A. (Asplundia) sp. nov.	89.3	8.0	2.7	10.7
Ca. palmata (n=107)	12.1	50.5	37.4	87.9
Cy. bipartitus (n=130)	53.8	38.5	7.7	46.2
D. crinitum (n=133)	90.2	9.0	0.8	9.8
D. dolichostemon	96.7	3.3	0.0	3.3
D. globosum	89.3	10.0	0.7	10.7
D. grandifolium	99.3	0.7	0.0	0.7

TABLE 4 *(continued)*

PERCENTAGES OF STOMATAL COMPLEXES IN THE ABAXIAL EPIDERMIS IN WHICH NEITHER, ONE, OR BOTH NONPOLAR SUBSIDIARY CELL(S) EXTEND(S) TO THE OUTER EDGE(S) OF THE ASSOCIATED CELL FILE(S).*

	Neither extends to outer edge	One extends to outer edge	Both extend to outer edge	One or both extend to outer edge(s) (column 2 + column 3)
D. harlingii	100	0	0	0
D. macrophyllum	95.3	4.7	0.0	4.7
D. mirabile	96.7	3.3	0.0	3.3
D. sp. nov. aff. *D. nanum*	91.3	8.7	0.0	8.7
D. rheithrophilum	90.0	9.3	0.7	10.0
D. schultesii	93.3	6.7	0.0	6.7
D. wallisii	99.3	0.7	0.0	0.7
D. sp. nov. (coll. A)	100.0	0.0	0.0	0.0
D. sp. nov. (coll. B)	92.0	8.0	0.0	8.0
E. funifer (n=122)	45.1	39.3	15.6	54.9
L. bierhorstii	92.0	7.3	0.7	8.0
L. integrifolia	18.0	49.3	32.7	82.0
L. lancifolia (n=134)	28.4	43.3	28.4	71.7
Sch. chorianthum	96.0	4.0	0.0	4.0

Sph. acutitepala	2.0	26.0	72.0	98.0
Sph. crocea	1.3	31.3	67.3	98.7
Sph. killipii (n=151)	15.2	48.3	36.4	84.7
Sph. snidernii (n=151)	39.1	46.4	14.6	60.9
Sph. woodsonii	47.3	40.0	12.7	52.7
Sph. sp. nov. aff. *Sph. woodsonii*	24.7	47.3	28.0	75.3
Sph. sp. nov.	53.3	40.0	6.7	46.7
St. anomala	8.0	37.3	54.7	92.0
St. stylaris (n=131)	11.5	47.3	41.2	88.5
T. bissectus (n=129)	25.6	45.0	29.5	74.5

*For each species, one-hundred and fifty stomata were examined in an epidermal peel, except where another number is indicated in parentheses after the species name. As often as possible in a peel, fields were studied which were laterally rather than vertically adjacent to one another, to maximize randomness of sampling. Observations of *Cy. bipartitus* were subject to error because longitudinal files of ordinary epidermal cells tend to be difficult to identify in this species.

TABLE 5

PERCENTAGES OF SPECIES IN WHICH LOW, MODERATE, OR HIGH PERCENTAGES OF COMPLEXES EXHIBIT ONE OR TWO NONPOLAR SUBSIDIARY CELL(S) WHICH EXTEND TO THE OUTER EDGE(S) OF THE ASSOCIATED CELL FILE(S)*

	Percentage of species with low percentages of such complexes (1–11%)	Percentage of species with moderate percentages of such complexes (12–44%)	Percentage of species with high percentages of such complexes (45–99%)
Asplundia (23, 94)	21.7%	69.6%	8.7%
Carludovica (1, 3)	–	–	100%
Cyclanthus (1, 1)	–	–	100%
Dicranopygium (13, 48)	100%	–	–
Evodianthus (1, 1)	–	–	100%
Ludovia (3, 3)	33.3%	–	66.6%
Schultesiophytum (1, 1)	100%	–	–
Sphaeradenia (7, 42)	–	–	100%
Stelestylis (2, 4)	–	–	100%
Thoracocarpus (1, 1)	–	–	100%

*In parentheses after the name of each genus are indicated the number of species considered, and the total number of species known, not including undescribed species collected by the writer.

TABLE 6

CONTACTS BETWEEN STOMATAL COMPLEXES

	Percentage of stomatal complexes in contact with one or more other stomatal complexes	Percentage of stomatal complexes which share subsidiary cells	Percentage of contacts which entail sharing of subsidiary cells (column 2/column 1)	Types of sharing of subsidiary cells by two adjacent stomatal complexes*
Asplundia pycnantha	50.3% (n=150 complexes)	2% (n=200 complexes)	4.0%	Type 1: 100% (n=2 pairs of complexes)
Carludovica palmata	64.2% (n=151)	–	–	–
Cyclanthus bipartitus	97.0% (n=131)	11% (n=200)	11.3%	Type 1: 54.5% Type 2: 27.3% Type 3: 18.2% (n=11)
Dicranopygium crinitum	49.1% (n=159)	2% (n=200)	4.1%	Type 1: 100% (n=2)
Evodianthus funifer	47.7% (n=155)	0% (n=200)	0%	0%
Ludovia lancifolia	4% (n=200)	0% (n=200)	0%	0%
Schultesiophytum chorianthum	66.9% (n=154)	2% (n=200)	3.0%	Type 1: 50% Type 2: 50% (n=2)
Sphaeradenia killipii	65.4% (n=153)	7% (n=200)	10.7%	Type 1: 100% (n=7)
Stelestylis stylaris	70.9% (n=182)	7% (n=200)	9.9%	Type 1: 85.7% (n=7) Type 3: 14.3%
Thoracocarpus bissectus	78.3% (n=143)	6% (n=200)	7.7%	Type 1: 33.3% Type 3: 66.6% (n=6)

*Types of sharing are defined by Wilder (in press *a*).

INTRODUCTION TO TABLES 7, 9–11
(Wilder, in press *b*)*

Within interridge areas and between boundary layers, portions of cyclanthaceous laminae exhibit either two (adaxial and abaxial) or three main regions of mesophyll (adaxial, middle, and abaxial; Table 7). The adaxial region is only sometimes a palisade region, whereas, the middle and abaxial regions are spongy mesophyll. Regions of mesophyll are distinguished mostly according to features of ordinary parenchyma cells. These cells may exhibit various ergastic materials, including starch, tannin, and different kinds of crystals. In certain species some cells also contain star figures, i.e., small or large stellate inclusions tentatively interpreted as tannin. In most species ordinary parenchyma cells are essentially monomorphic, but in two species of *Dicranopygium* these cells exhibit pronounced dimorphism (Table 8). Fibers occur in the mesophyll of all species studied, but differ quantitatively between various species (Tables 9–11). Parenchyma-like dead cells were observed in several and all species of the Asplundia group and Sphaeradenia group, respectively, but only such cells of the Sphaeradenia group exhibited conspicuously birefringent cell walls. Those dead cells with birefringent walls, therefore, constitute an extremely important systematic-anatomical character within the Cyclanthaceae.

*Table no. 8 is included in Wilder (in press *b*), where it is listed as Table 1.

TABLE 7

SPECIES WITH THREE MAIN REGIONS OF MESOPHYLL (ALL UNLISTED SPECIES HAVE TWO REGIONS).

A. cabrerae
A. cayapensis
A. gamotepala
A. moritziana
A. aff. *A. moritziana*
A. pycnantha
A. sp. nov. aff. *A. rhodea*
A. tetragona
A. aff. *A. vaupesiana* (coll. *A*)
Cy. bipartitus
E. funifer
L. lancifolia
Sph. snidernii
Sph. sp. nov. aff. *Sph. woodsonii*
St. stylaris
T. bissectus

TABLE 9

DATA PERTAINING TO FIBER STRANDS OF THE MESOPHYLL

Species	No. of fiber strands/mm width of interridge area (in parentheses are indicated no. of strands counted and width of portion(s) of lamina considered in mm, respectively)	Percentage of fiber strands on adaxial half of interridge area (in parentheses are indicated no. of strands counted on adaxial and both sides of lamina, respectively
A. aff. *A. antioquiae* (coll. *A*)	29 (189, 6.64)	55.0 (104, 189)
A. aff. *A. antioquiae* (coll. *B*)	28 (203, 7.24)	64.5 (131, 203)
A. cabrerae	83 (224, 2.72)	60.3 (135, 224)
A. cayapensis	49 (119, 2.45)	59.7 (71, 119)

TABLE 9 *(continued)*

DATA PERTAINING TO FIBER STRANDS OF THE MESOPHYLL

Species	No. of fiber strands/mm width of interridge area (in parentheses are indicated no. of strands counted and width of portion(s) of lamina considered in mm, respectively)	Percentage of fiber strands on adaxial half of interridge area (in parentheses are indicated no. of strands counted on adaxial and both sides of lamina, respectively
A. sp. nov. aff. *A. cupulifera* (coll. *A*)	39 (311, 8.01)	54.0 (168, 311)
A. sp. nov. aff. *A. cupulifera* (coll. *B*)	78 (510, 6.54)	55.5 (283, 510)
A. gamotepala	93 (210, 2.26)	56.7 (119, 210)
A. hookeri	17 (94, 5.58)	48.9 (46, 94)
A. longitepala	18 (78, 4.44)	69.2 (54, 78)
A. sp. nov. aff. *A. longitepala*	48 (224, 4.70)	55.8 (125, 224)
A. moritziana	26 (196, 7.45)	52.0 (102, 196)
A. aff. *A. moritziana*	20 (119, 5.93)	58.0 (69, 119)
A. sp. nov. aff. *A. multistaminata*	24 (91, 3.83)	58.2 (53, 91)
A. peruviana	46 (205, 4.41)	61.5 (126, 205)
A. pycnantha	65 (327, 5.06)	55.0 (180, 327)
A. quinindensis	49 (232, 4.73)	56.5 (131, 232)
A. sp. nov. aff. *A. rhodea*	32 (99, 3.06)	57.6 (57, 99)
A. rigida	28 (172, 6.13)	57.6 (99, 172)
A. tetragona	38 (158, 4.19)	51.9 (82, 158)
A. urophylla	19 (121, 6.55)	61.2 (74, 121)
A. aff. *A. vaupesiana* (coll. *A*)	92 (366, 4.00)	63.7 (233, 366)
A. aff. *A. vaupesiana* (coll. *B*)	24 (127, 5.23)	70.1 (89, 127)
A. (Asplundia) sp. nov.	28 (127, 4.61)	59.2 (109, 184)
Ca. palmata	66 (480, 7.26)	61.7 (296, 480)
Cy. bipartitus	5.8 (46, 8.00)	97.8 (45, 46)
D. crinitum	40 (176, 4.41)	55.1 (97, 176)

TABLE 9 *(continued)*

DATA PERTAINING TO FIBER STRANDS OF THE MESOPHYLL

Species	No. of fiber strands/mm width of interridge area (in parentheses are indicated no. of strands counted and width of portion(s) of lamina considered in mm, respectively)	Percentage of fiber strands on adaxial half of interridge area (in parentheses are indicated no. of strands counted on adaxial and both sides of lamina, respectively
D. dolichostemon	13 (48, 3.63)	58.3 (28, 48)
D. globosum	13 (93, 7.27)	46.2 (43, 93)
D. grandifolium	12 (55, 4.66)	58.2 (32, 55)
D. harlingii	4.3 (23, 5.31)	100 (36, 36)
D. macrophyllum	27 (111, 4.12)	36.0 (40, 111)
D. mirabile	5.7 (31, 5.46)	71.0 (22, 31)
D. sp. nov. aff. *D. nanum*	9.5 (89, 9.05)	96.6 (86, 89)
D. rheithrophilum	24 (153, 6.37)	56.2 (86, 153)
D. schultesii	20 (99, 4.91)	59.6 (59, 99)
D. wallisii	19 (139, 7.49)	64.7 (90, 139)
D. sp. nov. (coll. *A*)	8.0 (79, 9.83)	50.6 (40, 79)
D. sp. nov. (coll. B)	17 (132, 7.59)	44.7 (59, 132)
E. funifer	46 (154, 3.39)	56.1 (83, 148)
L. bierhorstii	13 (67, 5.25)	82.1 (55, 67)
L. integrifolia	29 (101, 3.47)	53.5 (54, 101)
L. lancifolia	75 (482, 6.41)	57.1 (275, 482)
Sch. chorianthum	24 (110, 4.62)	64.9 (72, 111)
Sph. acutitepala	56 (333, 5.91)	50.5 (168, 333)
Sph. crocea	27 (276, 10.2)	56.5 (156, 276)
Sph. killipii	73 (456, 6.25)	50.2 (229, 456)
Sph. snidernii	30 (171, 5.65)	53.8 (92, 171)
Sph. woodsonii	108 (209, 1.93)	58.9 (123, 209)
Sph. sp. nov. aff. *Sph. woodsonii*	49 (308, 6.26)	66.2 (204, 308)
Sph. sp. nov.	30 (188, 6.27)	41.0 (77, 188)
St. anomala	41 (185, 4.48)	60.0 (111, 185)
St. stylaris	38 (397, 10.4)	56.2 (223, 397)
T. bissectus	86 (684, 7.95)	56.5 (375, 664)

TABLE 10

CONCENTRATION OF FIBER STRANDS IN INTERRIDGE AREAS*

Genus	Percentage of species with low concentration (0–19.9/mm width)	Percentage of species with moderate concentration 20–49.9/mm width)	Percentage of species with high concentration (50–109.9/mm width)
Asplundia (23, 94)	13.0%	65.2%	21.7%
Carludovica (1, 3)			100%
Cyclanthus (1, 1)	100%		
Dicranopygium (13, 48)	69.2%	30.8%	
Evodianthus (1, 1)		100%	
Ludovia (3, 3)	33.3%	33.3%	33.3%
Schultesiophytum (1, 1)		100%	
Sphaeradenia (7, 42)		57.1%	42.9%
Stelestylis (2, 4)		100%	
Thoracocarpus (1, 1)			100%

*In parentheses after the name of each genus are indicated the number of species considered and the total number of species per genus, respectively (not including undescribed species presently studied).

TABLE 11

DATA PERTAINING TO FIBER STRANDS OF THE MESOPHYLL

	Percentage of fiber strands on both sides of lamina which are in subepidermal layers*	Percentage of adaxially situated fiber strands in adaxial subepidermal layer*	Percentage of abaxially situated fiber strands in abaxial subepidermal layer*	Mean numbers of hypodermal parenchyma cells intervening between adjacent pairs of fiber strands in adaxial subepidermal layer**
A. pycnantha	43.4 (334)	46.8 (190)	38.9 (144)	2.38 (50)
Ca. palmata	43.8 (482)	53.8 (296)	28.0 (186)	1.70 (50)
Cy. bipartitus	53.1 (49)	54.2 (48)	0 (1)	10.4 (23)
D. crinitum	31.9 (329)	34.2 (184)	29.0 (145)	4.72 (50)
E. funifer	79.9 (289)	82.7 (173)	75.9 (116)	1.46 (50)
L. lancifolia	48.5 (482)	48.4 (275)	48.8 (207)	1.40 (50)
Sch. chorianthum	75.4 (187)	68.3 (123)	89.1 (64)	3.68 (40)
Sph. killipii	83.1 (455)	79.9 (229)	86.3 (226)	1.06 (50)
St. stylaris	86.4 (397)	88.3 (223)	83.9 (174)	1.06 (50)
T. bissectus	29.1 (663)	38.0 (371)	17.8 (292)	2.14 (50)

*In parentheses are indicated number of fiber strands observed.
**In parentheses are indicated number of fiber strand pairs observed.

INTRODUCTION TO TABLES 12–13
(Wilder, in press *c*)

Within interridge areas and between boundary layers cyclanthaceous laminae exhibit raphide sacs and, sometimes, also styloid sacs and/or sacs intermediate between raphide and styloid sacs (Tables 12, 13). These crystal sacs normally lack chloroplasts, but at least sometimes contain leucoplasts and, apparently, normal nuclei. In raphide sacs the raphides usually comprise an orderly array, and are sometimes compound. Styloid sacs occur in *Evodianthus funifer* and all species studied of *Sphaeradenia* and *Stelestylis*, but are less common among remaining species of Carludovicoideae. In almost all species raphide and styloid sacs tend to be oriented along paradermal planes; however, in *E. funifer* the styloid sacs normally lie in all directions within the mesophyll. Scattered regions of periderm occur in various species, apparently, because of wounding. I have developed a concept of boundary layers. A boundary layer separates ordinary mesophyll tissue from another part of the plant. Cyclanthaceous laminae exhibit four types of boundary layers, viz., hypodermis, bundle sheath, epithelium of mucilage cavities, and laticifer sheath. All boundary layers exhibit significant features in common, in addition to position, including aspects of intercellular spaces between their constituent cells, and chloroplast position. In the adaxial hypodermis the shapes of hypodermal parenchyma cells in surface view are very predictable.

TABLE 12

KINDS OF CRYSTAL SACS PRESENT WITHIN INTERRIDGE AREAS OF CYCLANTHACEOUS LAMINAE.

Species	Raphide sacs not of boundary layers	Styloid sacs not of boundary layers	Subepidermal raphide sacs	Subepidermal styloid sacs
A. aff. *A. antioquiae* (coll. *A*)	+			
A. aff *A. antioquiae* (coll. *B*)	+		+	
A. cabrerae	+			
A. cayapensis	+(I)	+(I)		
A. sp. nov. aff. *A. cupulifera* (coll. *A*)	+(S)		+	
A. sp. nov. aff. *A. cupulifera* (coll. *B*)	+		+	
A. gamotepala	+			
A. hookeri	+(I)	+(I)	+	
A. longitepala	+			
A. sp. nov. aff. *A. longitepala*	+			
A. moritziana	+			
A. aff. *A. moritziana*	+		+	
A. sp. nov. aff. *A. multistaminata*	+			
A. peruviana	+		+	
A. pycnantha	+(S)		+	
A. quinindensis	+			
A. sp. nov. aff. *A. rhodea*	+		+	
A. rigida	+		+	
A. tetragona	+		+	
A. urophylla	+			
A. aff. *A. vaupesiana* (coll. *A*)	+		+	
A. aff. *A. vaupesiana* (coll. *B*)	+		+	
A. (Asplundia) sp. nov.	+			
Ca. palmata	+(I)	+(I)	+	+
Cy. bipartitus	+	+(Bu)	+	

TABLE 12 *(Continued)*

KINDS OF CRYSTAL SACS PRESENT WITHIN INTERRIDGE AREAS OF CYCLANTHACEOUS LAMINAE.

Species	Raphide sacs not of boundary layers	Styloid sacs not of boundary layers	Subepidermal raphide sacs	Subepidermal styloid sacs
D. crinitum	+		+	
D. dolichostemon	+(I)	+(I)	+	
D. globosum	+		+	
D. grandifolium	+			
D. harlingii	+		+	
D. macrophyllum	+		+	
D. mirabile	+			
D. sp. nov. aff. *D. nanum*	+(S)		+	
D. rheithrophilum	+		+	
D. schultesii	+			
D. wallisii	+			
D. sp. nov. (coll. *A*)	+			
D. sp. nov. (coll. *B*)	+		+	
E. funifer	+	+		+
L. bierhorstii	+		+	
L. integrifolia	+		+	
L. lancifolia	+		+	
Sch. chorianthum	+			
Sph. acutitepala	+	+		+
Sph. crocea	+	+		+
Sph. killipii	+	+	+	
Sph. snidernii	+	+		
Sph. woodsonii	+	+		+
Sph. sp. nov. aff. *Sph. woodsonii*	+	+		
Sph. sp. nov.	+	+	+	
St. anomala	+	+		+

TABLE 12 *(Continued)*

KINDS OF CRYSTAL SACS PRESENT WITHIN INTERRIDGE AREAS OF CYCLANTHACEOUS LAMINAE.

Species	Raphide sacs not of boundary layers	Styloid sacs not of boundary layers	Subepidermal raphide sacs	Subepidermal styloid sacs
St. stylaris	+	+		+
T. bissectus	+			

+ = present and well-defined.

+(I) = typical raphide sacs, styloid sacs, and all intermediates between these two cell types are present.

+(S) = some sacs have small numbers of crystals which mostly tend to be intermediate between raphides and styloids, but well-defined styloids are generally absent.

(Bu) = styloid sacs are mainly limited to bundle sheaths, where they occur together with raphide sacs and intermediate types of sacs.

TABLE 13

LENGTHS OF RAPHIDE BUNDLES AND STYLOIDS IN CLEARED LAMINAE (μm, MEASURED USING CROSSED POLARS)

	Raphide bundles of abaxial subepidermal layer*				Raphide bundles of adaxial subepidermal layer*				Raphide bundles of portions of mesophyll not belonging to boundary layers**				Styloids of portions of mesophyll not belonging to boundary layers**			
	Range	Mean	Standard Deviation	Sample	Range	Mean	Standard Deviation	Sample	Range	Mean	Standard Deviation	Sample	Range	Mean	Standard Deviation	Sample
Asplundia tetragona	23-50	36.7	7.11	25	23-48	35.4	4.95	25	52-407	229	94.0	20				
Dicranopygium dolichostemon	31-115	62.2	22	25	46-145	83.5	31.5	7	46-229	141	45.8	25	172-330	223	37.1	25
Dicranopygium harlingii	29-88	47.1	11.0	25	44-88	63.9	11.7	25	80-199	129	30.0	25				
Dicranopygium sp. nov. (coll. *B*)	31-84	52.4	13.4	25	42-86	65.2	10.0	25	94-153	118	15.8	25				
Ludovia bierhorstii	23-55	37.4	8.27	25	21-48	30.6	5.88	25	29-273	169	85.2	25				
Sphaeradenia sp. nov.	15-40	26.8	4.87	25	27-65	41.2	7.32	25	74-107	86.7	7.75	25	57-191	148	33.6	25

*In *D.* sp. nov. bundles of the adaxial and abaxial hypodermides are commonly oriented anticlinally or nearly so; only bundles with essentially paradermal orientations were measured.

**In *D. dolichostemon* with all intermediates between raphides and styloids, crystals were measured only if they were clearly raphides (very narrow crystals, generally many per bundle) or styloids (broad crystals, one to several per crystal sac). In *Sph.* sp. nov. some raphide bundles in the cell layer immediately beneath the adaxial hypodermis were oriented anticlinally or nearly so, and were not measured.

INTRODUCTION TO TABLES 14–16
(Wilder, in press *d*)

Interridge areas of cyclanthaceous laminae exhibit longitudinal veins and commissural veins which vary from transverse to oblique. In at least some species of the Asplundia group, but not all of the Sphaeradenia group, these longitudinal veins tend to be oriented nearest the abaxial surface of the lamina (Table 14). In many species longitudinal veins of interridge areas are of discrete orders, and up to a given order the number of veins of an order is twice, or nearly twice that of the next lower order (Table 15). Whereas, longitudinal veins of interridge areas are normally upright, commissures vary from upright to inverted. In ten species cleared portions of lamina each measuring 120 mm^2 exhibited from six to forty-seven commissures (Table 16). Expansion tissue and presumed expansion tissue develop in all species of Carludovicoideae and in *Cyclanthus bipartitus*, respectively. Adaxial and abaxial ridges are mostly associated with one or more longitudinal veins. The main vein of a ridge is normally upright, whereas, additional vein(s) may be upright or inverted to various degrees. In interridge areas and ridges longitudinal veins are normally collateral, but bicollateral, amphivasal, and amphicribal veins may also be present.

TABLE 14

POSITIONS OF LONGITUDINAL VEINS IN INTERRIDGE AREAS (CARLUDOVICOIDEAE) OR NONCOSTAL PORTIONS OF LAMINA (CYCLANTHOIDEAE) RELATIVE TO THE ADAXIAL AND ABAXIAL SURFACES OF THE LAMINA.*

	Percentage of veins situated nearest the abaxial surface	Percentage of veins situated ca. equidistant between the two surfaces	Percentage of veins situated nearest the adaxial surface
CYCLANTHOIDEAE			
Cyclanthus bipartitus (20)	100	–	–
CARLUDOVICOIDEAE			
ASPLUNDIA GROUP			
A. pycnantha (20)	100	–	–
Ca. palmata (20)	100	–	–
D. crinitum (20)	100	–	–
E. funifer (20)	95	5	–
Sch. chorianthum (18)	100	–	–
T. bissectus (20)	100	–	–
SPHAERADENIA GROUP			
L. lancifolia (16)	31	31	38
Sph. killipii (18)	39	–	61
St. stylaris (20)	80	5	15

*The number of veins considered is indicated

TABLE 15

MEAN PERCENTAGES OF THE EXPECTED NUMBERS OF LONGITUDINAL VEINS OF EACH ORDER PRESENT IN THE INTERRIDGE AREAS OF TWENTY-TWO SPECIES OF *ASPLUNDIA*, TEN OF *DICRANOPYGIUM*, AND FOUR OF *SPHAERADENIA*, AND STANDARD DEVIATIONS.* **

	First Order	Second Order	Third Order	Fourth Order	Fifth Order	Sixth Order	Seventh and Higher Orders
Asplundia (29)	100, 0	100, 0	98.9, 5.33	71.9, 33.4	15.3, 21.6	0.43, 1.46	0, 0
Dicranopygium (15.5)	100, 0	98.3, 5.28	90, 19.2	48.3, 37.9	5.63, 9.41	0, 0	0, 0
Sphaeradenia (4)	100, 0	100, 0	100, 0	68.8, 33.1	35.9, 35.5	1.56, 1.80	0,0

*The mean percentages for each genus were computed as follows. For every species the percentage of the expected number of veins present of each order was determined, based on a sample of one to several interridge areas. Then, the percentages for each order of vein were averaged for all species (the species being weighted equally, regardless of the number of interridge areas counted per species).

**In parentheses after the name of each genus is indicated the number of interridge areas examined of all species.

TABLE 16

NUMBERS OF COMMISSURES WITHIN 120 mm^2 OF LAMINA, AWAY FROM COSTAE*

SPECIES	NUMBER OF COMMISSURES
A. pycnantha	10
Ca. palmata	31
Cy. bipartitus	31
D. crinitum	47
E. funifer	12
L. lancifolia	10
Sch. chorianthum	45
Sph. killipii	10
St. stylaris	14–15
T. bissectus	6

*Branches of commissures were counted as separate commissures. For example, in a case where a commissure became divided into two parts at one end, the undivided portion and its two products were interpreted to represent a total of two commissures.

ACKNOWLEGMENTS

Initial stages of this study were done under a postdoctoral fellowship provided by the Cabot Foundation, Harvard University, and a concomitant appointment at the Fairchild Tropical Garden, Miami, Florida. Funds were also obtained from National Science Foundation grants BSR-82-10618, 78-04731, and GB31844X. Additional support for travel came from the Atkins Funds and Cabot Foundation of Harvard University and the Research Board of the University of Illinois at Chicago Circle.

I am deeply grateful to Dr. P. B. TOMLINSON of Harvard University for his invaluable help, rendered on numerous occasions. I am indebted, too, to Dr. GUNNAR HARLING of the University of Göteborg for his encouragement and help in identifying virtually all of the species presently studied. I also express deep appreciation to the following individuals and institutions for their assistance during this investigation: Dr. JOHN POPENOE and the Fairchild Tropical Garden; Dr. ROBERT DRESSLER and the Smithsonian Tropical Research Institute; Dr. R. A.

OWEN, Mr. RAMNARINE PERSAUD and the Forest Department of the Republic of Guyana; Dr. OMAWALE and the University of Guyana; Dr. JAIRO CORREA, Dr. JAIME RIVERA CASTRO, and the Universidad Nacional de Colombia, Medellín; Dr. ALVARO FERNANDEZ-PEREZ, Dr. ENRIQUE FORERO, and the Universidad Nacional de Colombia, Bogotá; Dr. ENRIQUE HERNANDEZ and the Universidad de Nariño, Pasto, Colombia; Dr. CIRO A. VALOYES, sectional head of Inderena, Quibdo, Colombia; Dr. JULIAN STEYERMARCK, Dr. GILBERTO MORILLO, Dr. ANGIL GONZALES, and the Instituto Botánico, Caracas, Venezuela; Dr. BASSETT MAGUIRE and the New York Botanical Garden; Dr. RICHARD SCHULTES and the Gray Herbarium, Harvard University, Mr. TOMAS QUIONES, mayor of Puerto Nariño, Colombia; Dr. WILLIAM BURGER and the Field Museum of Natural History.

In addition, the following individuals provided indispensable assistance: Mrs. REBECCA WILDER; Mr. JAIME MORENO; Mr. DENNIS MAGEE; Mr. EDUARDO CALDERON; MR. DANIEL HARRIS; Mrs. HELEN WOODEN; Mr. JEFFREY VINCENT; Ms. DOROTHY SMITH; and IGNACIO, ALVARO, CAROLYN, and DIEGO VILLA. Mr. WILLIAM ORMEROD duplicated my color transparencies with black-and-white film, and prepared prints; he also made the original photographs of specimens in figs. 1–4 in Wilder (in press *d*).

LITERATURE CITED

Tomlinson, P. B., and G. J. Wilder. 1984. Systematic anatomy of Cyclanthaceae (Monocotyledoneae) — an overview. Bot. Gaz.: in press.

Wilder, G. J. Anatomy of noncostal portions of lamina in the Cyclanthaceae (Monocotyledoneae). *I.* Epidermis. Bot. Gaz.: in press *a*.

______. Anatomy of noncostal portions of lamina in the Cyclanthaceae (Monocotyledoneae). *II.* Regions of mesophyll, monomorphic and dimorphic ordinary parenchyma cells, mesophyll fibers, and parenchyma-like dead cells. Bot. Gaz.: in press *b*.

______. Anatomy of noncostal portions of lamina in the Cyclanthaceae (Monocotyledoneae). *III.* Crystal sacs, periderm, and boundary layers of the mesophyll. Bot. Gaz.: in press *c*.

______. Anatomy of noncostal portions of lamina in the Cyclanthaceae (Monocotyledoneae). *IV.* Veins of interridge areas, expansion tissue, and adaxial and abaxial ridges. Bot. Gaz.: in press *d*.